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Review

Addressing the challenges of research on human-wildlife interactions using the concept of Coupled Natural & Human Systems

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ABSTRACT

With the global expansion of human populations, research on human-wildlife interactions (HWIs) has become increasingly important in conservation science. Despite its growing importance, such research faces challenges that include a bias towards evaluating wildlife- compared to human-related aspects of interactions, limited focus on the complexity of HWIs and their effects, assessments of more observable compared to hidden/subtle effects, and the lack of comparative studies. Here we review how the Coupled Natural and Human Systems (CNHS) approach has been useful to address these challenges. We demonstrate the relative dearth in studies that have implemented CNHS approaches in the context of HWIs, compared to human interactions with biophysical, abiotic, and other biotic natural systems. We next review conceptual CNHS frameworks implemented to model HWIs, their structural and functional similarities and differences, and reveal how they help to address some, but not all, of the afore-mentioned challenges. We then construct a general, integrated conceptual framework for human-wildlife CNHS borrowing elements from pre-existing frameworks, which includes a standardized designation/nomenclature of CNHS components and their relationships and builds on pre-existing frameworks by placing a greater emphasis on less visible outcomes of HWIs that remain under-represented in the CNHS literature. We discuss the potential and scope of this integrated framework in terms of its usefulness to address the above challenges, and the importance of moving human-wildlife CNHS frameworks from merely providing conceptual platforms towards their analytical utility as single 'whole' systems.

1. Introduction

Human wildlife interactions (HWIs) have existed throughout human evolutionary history and have consequences for both humans and wildlife (Dickman, 2010, 2012; Nyhus, 2016). The historically recent expansion of human populations and our activities have resulted in an unprecedented increase in HWIs. Their management is one of the most pressing conservation issues of the 21st century (Dickman, 2010, 2012; König et al., 2020; Nyhus, 2016).

Many studies have described and assessed interactions between humans and wildlife across a variety of landscapes: urban cities, agricultural fields, the buffer zones around wildlife sanctuaries and national parks (Dickman, 2012; Redpath et al., 2013). HWIs are defined here as *the juxtaposition or behavior of humans and wildlife towards each other in areas where they geospatially overlap* (Nyhus, 2016). Both within and across such 'interfaces', i.e. zones of overlap between humans and

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wildlife (Riley, 2007), HWIs can vary broadly in form and frequency. Such variation may impact both humans and wildlife by imposing adverse effects that may result in conflict, and/or neutral or even uplifting/positive effects that underlie their mutual coexistence[1] (Woodroffe et al., 2005; Nyhus, 2016; Peterson et al., 2010; Carter et al., 2012; König et al., 2020). For instance, human activities like habitat destruction, culling, or predation have been directly linked to wildlife population fragmentation and decline, disease acquisition, and extinction (Kahler and Gore, 2015; Loveridge et al., 2010; Cunningham et al., 2017). On the other hand, activities like habitat restoration and tourism that generates revenue may positively affect wildlife through population recovery and demographic stability (Carter et al., 2012). Likewise, for humans, increased contact or ecological overlap with wildlife can have both negative effects such as injuries and losses of crops and livestock (Treves et al., 2007) and emerging infectious disease risk (Cunningham et al., 2017; Nunn et al., 2008; Gryseels et al., 2020), as well as positive effects such as increased revenue and nourishment through ecosystem services (Ceauşu et al., 2019), tourism (Carter et al., 2012), and resource sharing (Carter et al., 2016). Such multifaceted effects are also complicated by differences across geographic locations and species in terms of how humans perceive and experience wildlife (Dickman, 2010; Treves et al., 2007).

Thus, HWIs impose costs-to-benefits tradeoffs to humans and wildlife, and thereby impact both in complex, sometimes paradoxical ways. Despite broad consensus, and extensive qualitative descriptions, regarding the multi-faceted nature of HWIs (Dickman, 2010, 2012; Nyhus, 2016), empirical studies of HWIs have nonetheless largely examined the impact of a small number of clearly observable forms of interactions (e.g., human provisioning of wildlife, mutual aggression, human culling or trapping of wildlife) on a single wildlife and/or human population. They have therefore lacked more holistic, comparative assessments (Dickman, 2010, 2012; Nyhus, 2016) that speak to nomothetic processes. Empirical research on HWIs would benefit from such approaches that examine the potential effects of sHWIs on the costs-benefits tradeoffs that underlie conflict and/or coexistence in both human and wildlife systems in equal measure. Such approaches are critical to understand the fundamental causal factors of HWIs, and to subsequently inform conservation efforts to either sustain on-going human-wildlife coexistence or implement interventions that aim to reconcile human activities with the needs of wildlife and vice-versa to move from conflict towards coexistence.

The Coupled Natural and Human Systems approach (CNHS), also interchangeably referred to as Social-Ecological Systems (SES) approach, promotes the consideration of human interactions with nature as a dynamic whole system (Liu et al., 2007; Ostrom, 2009; Wang et al., 2018; Colding and Barthel, 2019). This approach was novel at the time it was proposed because it considered both human and natural components simultaneously and proposed evaluating outcomes associated with both systems that emerge from these interacting components rather than focusing primarily on humans *or* wildlife. CNHS recognizes that multiple components of natural systems and human systems may influence human-environmental interactions, which may reciprocally feedback to impact the overall behavior and sustainability of both human populations and natural components (Carter et al., 2014; Liu et al., 2007; Ostrom, 2009; Wang et al., 2018). During the past decade, extensive research has focused on implementing CNHS approaches to largely develop 'frameworks', which conceptually model and/or quantitatively evaluate human interactions with natural systems generally (e.g., changes to natural landscapes, effects on freshwater or marine aquatic systems and hydrology, climate-change), and (to a lesser extent) HWIs and their feedback effects on human and wildlife systems more specifically (reviewed below). Nonetheless, the pioneering studies of HWIs as CNHS have resulted in the development of conceptual frameworks that remain largely system- or even taxon-specific, that address some but not other challenges facing research on HWIs, lack cross-framework consistency in their adherence to standardized CNHS terminology and designation of components, and primarily remain theoretical or conceptual rather than deployed to generate empirical or quantitative observations. The goals of this review are therefore threefold. First, we demonstrate how, despite the growing popularity of CNHS studies, there are few studies that have implemented CNHS to conceptually model human-wildlife systems compared to other human-natural systems. Second, we review previous studies of HWIs that use CNHS frameworks, and, through summarizing their similarities and differences, reveal how they have addressed some but not other gaps and challenges facing research on HWIs. Third, we construct an integrated, general human-wildlife CNHS framework that builds on and adds to these previous efforts, is broadly applicable across human-wildlife interfaces, and creates the opportunity to address the gaps and challenges in fundamental[2] HWIs research.

2. The challenges facing research on HWIs

To date, major challenges remain in our scientific understanding of HWIs, specifically with regard to the causal factors that generate these interactions and their impact on human and wildlife systems. The literature points to four major challenges (Table 1). First, a disproportionate number of studies on HWIs have focused on quantitatively evaluating human impact on wildlife systems, and not on quantifying wildlife impact on human systems (Barua et al., 2013; Dickman, 2010; Petersen et al. 2010; Kansky et al., 2016). This orientation is surprising given the anthropogenic bias in researchers' rhetoric to describe HWIs and their effects over the years (Peterson et al., 2010; Treves and Santiago-Ávila, 2020). Recognizing this, conservation biologists are increasingly studying the 'the human dimensions' of HWIs (Barua et al., 2013; Kansky et al., 2014, 2016; Karanth et al., 2018). This includes studies of how HWIs influence, or are influenced by, human attitudes and beliefs (Kansky et al., 2014, 2016), monetary and health-related costs and benefits (Barua et al., 2013; Dickman, 2010; Karanth et al.,

Table 1
Gaps and challenges facing research on human-wildlife interactions.

I	Imbalance between the consideration and operationalization of wildlife and human components
II	Limited knowledge or integration of the complexity of HWIs and their effects, and the rhetorical bias towards 'conflict' or 'coexistence'
III	More evaluations of observable effects at higher organizational levels, compared to subtle/hidden effects on the behavior and health of individuals
IV	Dearth in comparative studies

[1] While conservationists have traditionally referred to HWIs as 'human-wildlife conflict', and/or lately 'human-wildlife coexistence', this terminology has been recently questioned. Researchers now acknowledge that using terms like 'conflict' and 'coexistence' to define HWIs is rhetorically powerful and may influence bias in human motivations and action (Peterser et al. 2010; Treves & Santiago-Avila 2020). They argue that terms like 'conflict' and 'coexistence' emerge from the impact of HWIs, specifically the costs and benefits they impose, on human and wildlifes. Agreeing with these schools of thought, we refrain from using terms like 'conflict' and 'coexistence' to define or describe HWIs as such, throughout this review.

[2] CNHS approaches have also focused on tracking the effects of invasive perturbations of human-wildlife systems, e.g. the implementation of conflict interventions and management of ecosystem services, aimed at increasing coexistence. Nonetheless, such efforts would first require a fundamental or 'baseline' understanding of HWIs and their effects. In this review, we therefore focus exclusively on how CNHS approaches are useful to address the challenges facing fundamental (rather than invasive) research on HWIs.

2018), and inter-community interactions between residents, stakeholders, and policy-makers (Dressel et al., 2018; Duvall et al., 2017). Despite this recent upsurge in evaluations of the human system, there is still disproportionately less research that focuses on human related aspects of HWIs and little work that evaluates their effects as an integrative whole.

A second knowledge-gap is related to our limited understanding of the complexity of HWIs and their effects. While research from multiple human-wildlife interfaces have unveiled the variant, multi-dimensional nature of HWIs (Nyhus, 2016), the causal mechanisms and processes that underlie such variation and their effects on human and wildlife systems remain unclear. For instance, HWIs are often studied as simple cause-effect relationships between one or a few features of humans or wildlife on specific types of HWIs (Nyhus, 2016). These have also been influenced by human-centric perspectives and rhetorical bias that define and categorically associate HWIs and their effects as being indicative of either conflict (historically) or co-occurrence/coexistence (more recently) (Woodroffe et al., 2005; Nyhus, 2016; Peterson et al., 2010; Carter et al., 2012; König et al., 2020; Treves and Santiago-Ávila, 2020). In reality, HWIs can be complex insofar as they are multidimensional and spatiotemporally dynamic, and, for the same human-wildlife system, can involve a wide range of interactions that may be influenced by multiple external and internal characteristics of both humans and wildlife (Dickman, 2010; Nyhus, 2016). Thus, HWIs affect humans and wildlife through imposing complex costs-benefits-tradeoffs mechanisms, that lead to effects that may indicate the *extent of* conflict versus coexistence along a continuous rather than a dichotomous scale (Woodroffe et al., 2005; Nyhus, 2016; Peterson et al., 2010; Carter et al., 2012).

Third, studies of HWIs tend to focus on overt, observable interactions and their consequences (e.g., direct interactions like aggression and provisioning, culling, etc.) rather than the more subtle forms (e.g., health) (Dickman, 2010, 2012; Barua et al., 2013). Associated with this is the fact that the effects of HWIs on wildlife systems have often focused on the population or the species level, with fewer efforts focusing on inter-individual variation in responses to interactions with humans. For instance, some observable outcomes of HWIs in wildlife include heightened levels of aggression (e.g., sharks: Clua et al., 2010; reptiles: Uyeda et al., 2015; nonhuman primates: Southwick et al., 1976), changes in dietary preference (e.g., black bears, *Ursus americanus*: Lischka et al., 2018), the splitting of animal populations due to habitat fragmentation (Debinski and Holt, 2000), population declines and recovery (e.g., tigers, *Panthera tigris* and giant pandas, *Ailuropoda melanoleuca*: Carter et al., 2014), and species extinction events (e.g., Tasmanian tigers, *Thylacinus cynocephalus*: Paddle, 2002). In humans, HWIs may lead to observable outcomes such as losses or transactional costs associated with property or livestock (Treves et al., 2007) and socioeconomic gains and upliftment through activities like ecotourism and resource-sharing that in turn affect inter-community conflict versus tolerance and cooperation (Barua et al., 2013; Carter et al., 2012; Karanth et al., 2018). In comparison to such well documented outcomes, more subtle outcomes like changes to the behavior and health of individual humans and wildlife remain less well-studied (Barua et al., 2013; Kansky et al., 2014, 2016; Lischka et al., 2018).

A fourth challenge is related to identifying the common aspects of interactions and their effects across human-wildlife interfaces and distinguishing such general patterns from interface-specific effects. The majority of studies of HWIs have been conducted at a single location, and often within a short time-span (Carter et al., 2016; Dickman, 2012; Nyhus, 2016), calling into question the generalizability of the results. Comparative studies are needed to better understand the mechanisms that generate HWIs and the relative nature of their resultant costs and benefits, and thereby help construct and test generalizable hypotheses across spatiotemporal scales (Carter et al., 2014). This will lead to the design and catering of strategies related to decreasing conflict and increasing coexistence to either be specifically applicable within a location, or more broadly applicable across locations.

3. Coupled Natural and Human Systems (CNHS) approaches

One way to address the challenges detailed above is to use an approach that considers the human and wildlife systems equally and concurrently; CNHS approaches do just that (Carter et al., 2014; Liu et al., 2007; Ostrom, 2009; Wang et al., 2018) and offer promise for speeding the science of HWIs and addressing its challenges to date (Table 1). CNHS approaches view human interactions with nature as complex systems, in which multiple natural and human components are integrated as a whole (Fig. 1) and modeled as such. Historically, social scientists have focused heavily on human interactions more so than environmental influences, whereas ecologists have focused on pristine environments wherein humans are not considered, or at best remain peripheral agents. CNHS approaches encourage the integration of broad, interdisciplinary sciences aside from sociology and ecology – e.g., anthropology, geography, psychology – in evaluating human-environmental interactions. Using a CNHS approach, human (social) and natural (ecological) domains, rather than as separate entities, are conceptualized as being interconnected entities that form webs of interactions. One or more *components* of human systems are expected to interact with one or more components of natural systems. These latter effects, therefore, arise through reciprocal or feedback mechanisms referred to as *between-systems couplings* (Fig. 1). Furthermore, some components of both natural systems and human systems may directly influence, and be influenced by, other components within the same system. These mechanisms are referred to as *within-systems couplings* (Fig. 1).

The last decade has seen an exceptional increase in CNHS approaches being implemented to conceptualize, or (less so) quantitatively evaluate human interactions with nature (Wang et al., 2018). These studies have advanced research on human-environmental interactions in fundamentally important ways. Historically, empirical assessments of human-environmental interactions have tended to focus on the impact of one or a few components of a social (human) system on one or a few components of an ecological (natural) system, or vice-versa. There has also been an imbalance in the consideration of natural versus human components. CNHS approaches have played a major role in addressing this reductionism and imbalance; they have explicitly acknowledged that both natural systems and human systems are interlinked, and must therefore be assessed concurrently and modeled together (Table 1:I). CNHS studies place an inherent focus on considering not only multiple natural/ecological variables (e.g., natural landscape features, water quality, biodiversity, wildlife abundance) and social/human variables (e.g. socioeconomic factors, demographics, policy-making and governance, attitudes and beliefs), but also variables that define human-nature interlinkages (e.g. natural resource collection, harnessing ecosystem services, HWIs), and their feedback effects on natural and human components (Table 1:I, II).

Another advancement is that CNHS studies operate in unbiased ways because they do not assume directionality of effects. Their inherent emphasis on feedback mechanisms and coupling effects mean that CNHS approaches allow for a research-driven, unbiased understanding of human-nature interactions and their effects on the stability and sustenance of human and natural components, rather than perpetuating pre-existing biases that may influence our perspectives on human-nature interactions as being detrimental/costly versus (in some cases) beneficial to humans or the environment (Table 1:II). For instance, people from different societies have different worldviews of what it is to be human. Rather than perpetuating a specific worldview, CNHS would assign differences in worldviews as attributes and features of the human system that might affect human-environmental interactions, and/or establish such differences as being outcomes of these interactions.

Lately, CNHS studies have evolved to include more subtle aspects and effects of human-environmental interactions that are operational or measurable at the individual level (Table I:III). This has coincided with the recognition that there is a general dearth in knowledge of the

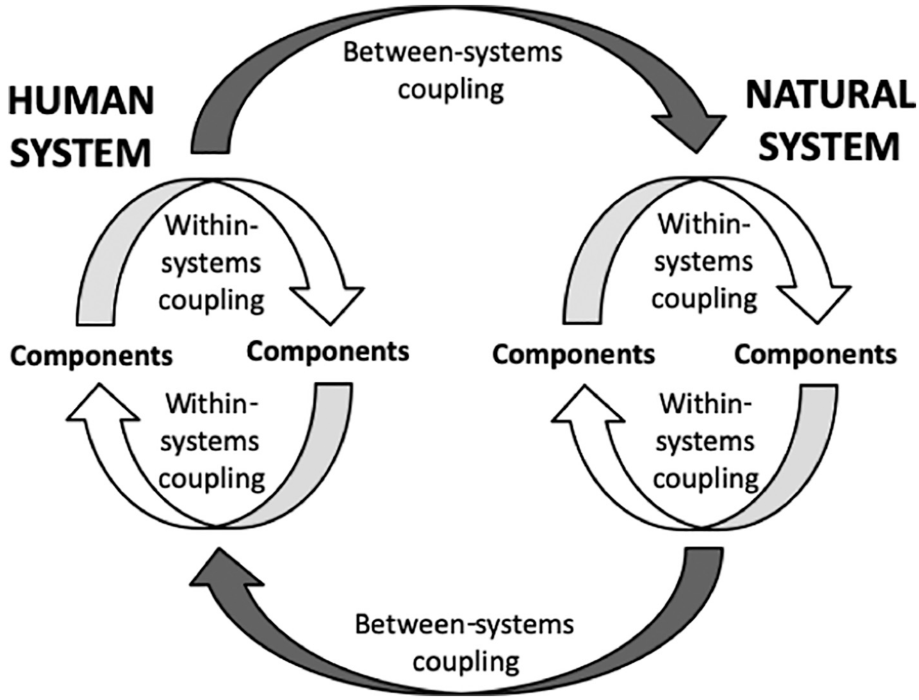

Fig. 1. Coupled Natural and Human Systems (CNHS).

attributes and (in particular) behavior of individual people who impact, or are impacted by, the environment (An, 2012; Noel and Cai, 2017). Shifting away from a stronger focus on macroscale effects of human activity (e.g., interlinkages between human community-level changes to governance and natural resource-management and resultant environmental shifts), CNHS approaches have increasingly begun to focus on more subtle microscale properties such as the behavior and decision-making of individual people (An, 2012; Noel and Cai, 2017). They have done so through a combination of fine-grained sampling approaches that collect data on the attributes, behavior, and decision-making of individuals, and using such data to construct mathematical agent-based models that assign individual or 'agents' into specific classes based on their social or ecological role (e.g., farmers, water users) and simulate how their decision-making impacts, and is in turn impacted by, changes to environmental or natural components (An, 2012; Noel and Cai, 2017). Thus, CNHS studies offer the scope to evaluate how heterogeneity in individual human behavior may underlie macroscale effects, and thereby affect the emerging performance of both human and natural systems (Table 1:III).

Another important advancement of CNHS approaches is the scope they offer for conducting comparative studies (Table 1:IV), through their regular construction and (at times) operationalization of 'conceptual frameworks'. Frameworks are important 'building-blocks' developed by researchers that enable testing ideas, specifically the mechanisms and processes through which entities may be interlinked, across contexts rather than being contained within specific contexts (Epstein et al. 2013; Ostrom, 2009). One way to think of frameworks is as conceptual models to which empirical data can be fitted – a first step in theory building. The last decade has seen a significant increase in the conceptualization and modeling of 'CNHS frameworks'. CNHS frameworks vary broadly in terms of their origin, purpose, structure, perspective (i.e., eco-centric versus anthropocentric), their organizational level(s) of focus, and use of terminology and nomenclature to classify CNHS components and interlinkages (Binder et al., 2013; examples of human-wildlife CNHS frameworks reviewed below). Despite such variation, all CNHS frameworks converge in some fundamental ways: having structural and coupling properties, including both natural and human components, assigning interlinkages that connect components both within and across systems, and catering to tackle the problem of evaluating human impact on the environment and vice-versa. Thus, CNHS frameworks, particularly when adhering to a standardized structure and designation/nomenclature of components and their interlinkages, can provide a solid platform for conducting comparative studies of human-environmental interactions and their effects (Liu et al., 2007; Carter et al., 2014, 2016; Wang et al., 2018; Table 1:IV).

4. Methods – a literature review of CNHS studies by area of focus

To better illustrate the distribution of major research areas that have implemented CNHS approaches, we conducted a search of the Web of Knowledge (WoK) database (www.webofknowledge.com). We searched for articles with a CNHS focus during the last decade (years 2011–2020) by entering the following boolean expression into the *Advanced Search* box:

(((Title=((coupled AND natural AND human AND system) OR (social-ecological AND system))) AND ((Abstract=((coupled AND natural AND human AND system) OR (social-ecological AND system))) OR (Author Key-words=((coupled AND natural AND human AND system) OR (social-ecological AND system))))))

The results yielded a total of 516 articles which included the words 'coupled', 'natural', 'human' and 'system(s)', or the words 'social-ecological' and 'system(s)' in their title, abstract and/or as author-specified key words. Of these, we identified 88 articles as being broad reviews of CNHS, of either terminology or empirical studies. We subdivided the remaining 428 articles into 13 categories based on the primary type(s) of natural component(s) that they either described and/or quantitatively evaluated. The results of this categorization are summarized in Fig. 2. They reveal that over the last decade (2011−2020), CNHS studies have heavily focused on human interactions with terrestrial features related to land-use (rural and urban development: 10.9% of articles, restoration of forests and other protected areas: 6%, food-production, agriculture, and livestock management: 16.9%), and abiotic factors (fresh-water systems and hydrology: 10.1%, coastal and ocean systems: 11%, atmospheric composition and climate change: 3.1%). A small fraction - 2.3% of articles - have focused on large-scale human-induced 'natural' disasters such as floods and wildfires. With

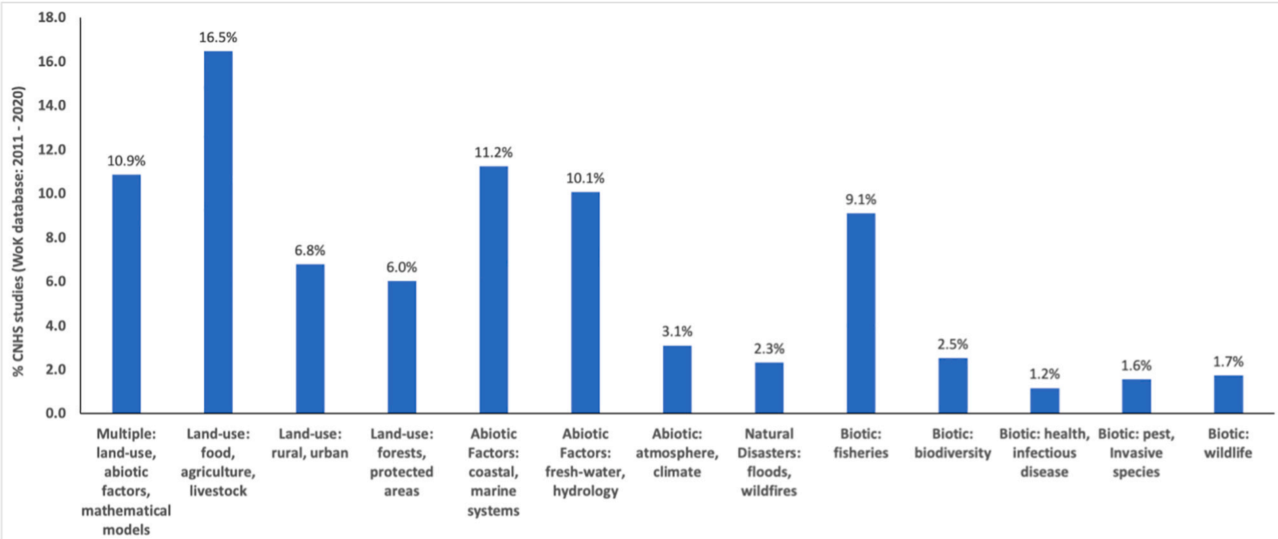

Fig. 2. Results of our search of the *Web of Knowledge (WoK)* database for studies between 2011 and 2020 that have proposed/implemented CNHS or SES frameworks. Values above bars indicate the % of total shortlisted articles (428, not including 88 review articles) under each category of natural systems studied.

the exception of fisheries and ocean harvests that show comparable numbers with land-use and abiotic factors (9.1% of articles), relatively few CNHS articles have focused on biotic natural components (biodiversity surveys: 2.5%, pest and invasive species management: 1.6%, health and infectious disease: 1.2%, interactions with wildlife: 1.7%). This demonstrates the relative dearth in studies that have implemented CNHS approaches in the context of HWIs.

5. A review of human-wildlife CNHS frameworks

Our literature review identified eight human-wildlife CNHS studies that have each illustrated (through a figure) their own CNHS framework that vary in their goals, the components studied, and their interrelationships. In this section, we provide an overview of these frameworks primarily in terms of their (i) overall purpose (including their primary human and wildlife components) and origin (in terms of the data used for the construction and any associated biases), (ii) structure and composition, and (iii) demonstrated/illustrated scope (Table 2). In the following section, we summarize the similarities and differences across these frameworks in the context of their utility in addressing the afore-mentioned challenges of HWI research.

The majority of these CNHS frameworks (five out of eight: Table 2) have been constructed for a specific wildlife taxon or social-ecological role, specifically apex-predators, flagship species, or primary grazers that provide or affect ecosystem services. Carter et al. (2017) present a balanced (in terms of its equal focus on human and wildlife system components) CNHS framework for illegal human poaching of large carnivores, in which they summarize how microscale components (i.e., the attributes and behavior of individual humans and wildlife) that are nested within higher-order or macroscale societal (human) and ecosystem (natural) components may impact, and reciprocally be impacted by, human poaching of large carnivores. Into this framework, they fit findings from previous studies of tigers and wolverines (*Gulo gulo*). For tiger populations in Laos, they illustrate how changes to human behavior as a response to increased societal regulation of hunting and tiger densities may explain an increase (rather than an expected decrease) in human poaching of tigers. The resultant tiger population declines lead to more compromised human interventions to strengthen law enforcement. For wolverines in Sweden, on the other hand, Carter et al. (2017) used the same framework to illustrate how compensation for reindeer loss and den site preservation, despite herders' location of wolverine den sites leading to an increase in poaching opportunities, may result in a decrease in hunting rates culminating in an increase in wolverine population sizes, predation rates of reindeer, and more compensations that improve human livelihood.

For conserving the Greater Sage grouse (*Centrocercus urophasianus)*, Duvall et al.'s (2017) framework focused specifically on how increasing the knowledge of local humans about grouse conservation through their involvement via workshops and interactions with technical advisory committees may increase habitat quality and grouse population density, and reciprocally increase inter-stakeholder interactions aimed at local sustenance and employment opportunities. Although their framework includes both human and wildlife components, it carries an anthropocentric bias in terms of the researchers relying primarily on data collected from interviews of key human informants to construct this framework. Rather than providing an illustration of a human-wildlife CNHS using previously estimated human and wildlife variables, its purpose was to provide a framework of interlinkages between key variables whose incumbent evaluations may be critical for future assessments of human-grouse interactions as CNHS. Although individual humans were interviewed in the study, this framework places a stronger focus on macroscale aspects of wildlife (e.g., grouse population density) and humans (e.g., community-stakeholder interactions), compared to individual-level microscale properties.

Two studies presented CNHS frameworks focusing on apex predators within marine ecosystems. Meek (2011) present a framework to reveal how human activities like seal hunting and offshore drilling generate regime shifts in polar bears (*Ursus maritimus*) and (consequently) other marine macroscale (ecosystem) components that bears affect. These effects reciprocally have long-term consequences for the subsistence and economic benefits of indigenous communities that overlap with bear home-ranges. As in Duvall et al.'s framework for sage-grouse, there is a greater emphasis on macroscale compared to microscale components of human and bear systems. However, CNHS components are included based on both human interviews in the same study, as well as findings from previous bear-centric studies, thereby avoiding anthropocentric or eco-centric bias in origins. Hessing-Lewis et al. (2018) present a CNHS framework to discuss how a more holistic understanding of the top-down effects of sea otters (*Enhydra lutris*) on marine ecosystems. Taking an eco- or wildlife-centric perspective, their framework is presented following an empirical evaluation of the ecological factors that predict otter foraging pressure on sea-grass, to speculate how otter foraging may alter marine ecosystem services that affect human societal features and quality of life, and thereby reciprocally impose environmental stressors

Table 2
Summary of eight previously constructed human-wildlife conceptual CNHS frameworks.

	Purpose & origins				Structure & composition			Demonstration & operationalization	
Study	Overall goal	Wildlife taxon illustrated on, or constructed for	Bias in origins	Data source(s)	Inclusion of both wildlife & human components	Inclusion of feedbacks & within-systems interlinkages	Structure & organizational level(s) of focus	Constructed or illustrated for more than one human-wildlife system	Operationalized as a whole
Carter et al. (2017)	Taxon-specific	Tigers & (*Panthera tigris*) Wolverines (*Gulo gulo*) as apex predators	Balanced	Illustrated using empirical evidence from prior studies	Yes	Yes	Nested & bidirectional; Microscale - > Macroscale (individuals - > ecosystems/ societies)	Yes (two taxa with similar social-ecological roles, i.e. large carnivores)	No
Duvall et al. (2017)	Taxon-specific	Greater sage-grouse (*Centrocercus urophasianus)* as keystone species	Anthropocentric (human decision-making and attitudes to impact HWIs and generate feedback effects on both systems)	Constructed based on human interviews in the same study, & empirical evidence from prior studies	Yes	Yes	Linear & bidirectional; Macroscale[a] (wildlife populations/ ecosystems, human communities/ societies)	No	No
Meek (2011)	Taxon-specific	Polar bears (*Ursus maritimus*) as marine apex predators	Balanced	Constructed based on human interviews in the same study, & empirical evidence from prior studies	Yes	Yes	Linear & bidirectional; Macroscale[a] (wildlife populations/ ecosystems, human communities/ societies)	No	No
Hessing-Lewis et al. (2018)	Taxon-specific	Sea otters (*Enhydra lutris*) as marine apex predators	Ecocentric (wildlife activities and behavior to impact HWIs and generate feedback effects on both systems)	Constructed based on ecological & behavioral data analyzed in the same study, & empirical evidence from prior studies	Yes	Yes	Linear & bidirectional; Macroscale (wildlife populations/ ecosystems, human communities/ societies)	No	No
Dressel et al. (2018)	Taxon-specific	Moose (*Alces alces*) as primary grazers	Balanced	Constructed using empirical evidence from prior studies, & operationalized using principle components analysis and geospatial mapping of a sub-set of human and wildlife components	Yes	Yes	Linear & bidirectional; Macroscale (wildlife populations/ ecosystems, human communities/ societies)	No	No
Carter et al. (2014)	General	Tigers & (*Panthera tigris*) Pandas (*Ailuropoda melanoleuca*) as keystone species	Balanced	Illustrated using empirical evidence from prior studies	Yes	Yes	Linear & bidirectional; Macroscale (wildlife populations/ ecosystems, human communities/ societies)	Yes (two taxa with similar social-ecological roles, i.e. keystone species)	No
Morzillo et al. (2014)	General	Rodents (order: *Rodentia*) as urban generalist omnivores	Anthropocentric (human attributes are the main drivers of HWIs and their feedback effects on both systems)	Illustrated using empirical evidence from prior studies	Yes	Yes	Nested & bidirectional; Microscale - > macroscale (individuals - > ecosystems/ societies)	No	No
Lischka et al. (2018)	General	Black bears (*Ursus americanus*) as urban	Balanced	Illustrated using empirical evidence from prior studies	Yes	Yes	Nested & bidirectional; Microscale - > macroscale (individuals - >	No	No

(*continued on next page*)

Table 2 (*continued*)

	Purpose & origins				Structure & composition			Demonstration & operationalization	
Study	Overall goal	Wildlife taxon illustrated on, or constructed for	Bias in origins	Data source(s)	Inclusion of both wildlife & human components	Inclusion of feedbacks & within-systems interlinkages	Structure & organizational level(s) of focus	Constructed or illustrated for more than one human-wildlife system	Operationalized as a whole
		generalist omnivores					ecosystems/ societies)		

[a] Study involved conducting surveys on individual people.

on marine ecosystem features that negatively impact trophic cascades. Again, the CNHS components included are largely macroscale ecosystem (natural) or societal (human) components.

Focusing on interactions between humans and grazing herbivores, specifically moose (*Alces alces*) populations in Sweden, Dressel et al. (2018) presented a CNHS framework in which they included a balanced, exhaustive set of macroscale variables pertaining to humans and wildlife. Like in the other human-wildlife CNHS frameworks reviewed here, the authors did not operationalize the feedback couplings illustrated in their framework. Nonetheless, they implemented Principal Component Analysis and GIS mapping to assess the co-occurrence of a sub-set of human and wildlife related variables. This revealed critical geospatial differences in the relative importance of natural (i.e., abundance of predators, other competing grazers) versus human (i.e., private versus government ownership of property) components in influencing both moose population densities and human establishment of moose management units.

A minority of studies (three out of eight: Table 2) have constructed general rather than taxon-specific CNHS frameworks, prior to illustrating these frameworks using previously collected data on specific 'case-study' human-wildlife systems. Carter et al. (2014) present a balanced human-wildlife CNHS framework based on dynamic and reciprocal relationships and predominantly macroscale effects. They illustrate this using data from prior studies on human interactions with keystone species, specifically tigers in Nepal and giant pandas in China. Aspects of human systems, such as the sizes and socioeconomic status of residential dwellings, employment, and tourism opportunities, through influencing human dependency and impact on forest (natural) resources, may impact tiger and panda population densities. In turn, changes to wildlife population densities, both through their top-down ecosystem effects and their effects on human system components like livestock and tourist activity, may detrimentally (but sometimes beneficially) feedback to impact the human system through affecting resources and revenue.

Morzillo et al. (2014) present an "emerging" anthropocentric framework, in which the characteristics of individual humans are posited to be the main driver of human-wildlife interactions and their feedback effects on the "emergent" attitudes and behavior of individual people and (thereby) wildlife presence in the area. Although linear rather than embedded or nested in structure, this framework nevertheless accounts for how some microscale effects like individual human behavior, are interlinked to macroscale variables like landscape changes, land use, and environmental policy. They use their framework, along with pre-existing data on the geospatial mapping of human surveys regarding pest-control behavior, to conceptualize human-rodent (order *Rodentia*) interactions and their coupled effects in urban areas of California. Attributes of individual humans, along with the presence of rodents, are the main drivers of human use of pest-control "rodenticides", the effects of which are likely to change human attitudes and behavior towards wildlife. Subtle attitudinal changes may influence, and be influenced by, more overt effects at higher organizational levels, such as changes to urban landscapes (humans) and the geospatial distribution and demographics of rodent populations (wildlife).

Lischka et al. (2018) present a nested, multi-level framework, which places a balanced emphasis on the effects of humans on wildlife and vice-versa (between-systems effects) across multiple, embedded organizational levels (individuals -> ecosystems/societies) that also influence each other (within-systems effects). They illustrate their framework using data from prior studies on interactions between black bears (a generalist omnivore) and human communities in peri-urban environments. Attributes of individual wildlife (e.g., bear boldness) and humans (e.g., demographic characteristics), may influence HWIs (e.g., human sightings of bears, bear foraging on garbage), which then reciprocally influence the behavioral activities and fitness of both individual wildlife (e.g., bear hibernation time, reproductive output) and humans (e.g., attitudes, trash management), and in turn other outcomes at higher organizational levels (e.g., abundance and distribution of bear populations, human establishment of house-owner associations).

The human-wildlife CNHS frameworks reviewed above demonstrate that scholars are increasingly considering aspects of both human and wildlife systems in trying to understand the origins of HWIs and their feedback effects on both humans and wildlife. Yet, each conceptual framework is structurally and functionally unique, in terms of their overall purpose of construction, origins of the data used, prioritization on what aspects of human and wildlife systems are included, organizational level(s) of focus, and demonstration in terms of the human-wildlife system of focus (Table 2). In the next section, we provide an in-depth summary of these frameworks with relation to the challenges facing research on HWIs (Table 1), and specifically focus on how CNHS frameworks applied to HWIs to-date have offered the scope to address some of these challenges more so than others.

6. CNHS applied to HWIs: the roads less travelled

Table 2 provides a summary of the similarities and differences between the above reviewed human-wildlife CNHS frameworks. Through reviewing these similarities and differences, here we summarize how these frameworks have been more useful in addressing some of the challenges facing research on HWIs presented in Table 1, but less so others.

A critical gap in research on HWIs concerns a prevailing imbalance in the consideration and operationalization of human and wildlife system components (Table 1:I). In theory, all the CNHS frameworks converge in that they address this gap in concept or theory, through their incorporations of both human and wildlife components in near-equal measure. Although two frameworks carry anthropocentric bias (Duvall et al., 2017; Morzillo et al., 2014), and one eco-centric bias (Hessing-Lewis et al., 2018), these biases, rather than preferential inclusion of more human compared to wildlife components or vice-versa, concern which set of components (human or wildlife) may act as the primary drivers of HWIs.

The second challenge pertains to studies recognizing, but not accounting for, the complex nature of HWIs and the mechanisms that underlie their feedback effects on humans and wildlife, and the resultant rhetorical bias in HWI studies that characterize HWIs as 'conflict' or 'coexistence' based on a single (type of) effect (Table 1:II). All eight frameworks theoretically or conceptually address the inherent complexity of HWIs, by including (1) multiple (rather a single) types of interactions (acknowledging that some interactions impact the human system more than the wildlife system or vice versa) that are initiated by both humans and wildlife (e.g., tiger livestock predation and human-induced habitat loss by Carter et al., 2014; moose browsing and human shooting by Dressel et al., 2018). Moreover, all frameworks include (2) dynamic mechanisms and processes, i.e. bi-directional or unidirectional but cyclic arrows as part of their structure linking various system components, to indicate within- and between-systems inter-linkages that underlie HWIs and their effects on both humans and wildlife (Table 1:II). Rather than resorting to rhetorical bias, and perpetuating a preconceived view of HWIs as 'conflict' or 'coexistence', these frameworks provide a platform for conducting fundamental, research-driven assessments of the *extent* of conflict versus co-existence through accounting for the dynamic nature of HWIs, their feedback mechanisms, and their resultant multivariate effects on humans and wildlife (Table 1:II). Such assessments, rather than pre-emptively categorizing HWIs as such of being indicative of either conflict or coexistence, also perpetuate a shift towards a more outcome- rather than an interaction-based assessment of the *extent* of conflict versus coexistence. For example, while the application of Carter et al.'s (2017) CNHS framework, through emergent feedback processes and outcomes, indicated compromised sustenance and a resultant increase in conflict as a consequence of human-tiger interactions in Laos, applying the same framework to human-wolverine interactions in Sweden suggested that feedback processes and outcomes would likely increase (rather than decrease) sustenance thereby suggesting that coexistence would override conflict in this system.

In comparison to Challenges I and II, however, only a minority of these conceptual frameworks offer the scope to address Challenges III and IV. Consistent with traditional research on HWIs, the majority of human-wildlife CNHS frameworks focus on macroscale effects of HWIs at higher organizational levels (Table 1:III), e.g. wildlife population demographics and/or home ranges (Carter et al., 2014; Dressel et al., 2018), the trophic effects of wildlife on their ecosystems (Hessing-Lewis et al., 2018), human socioeconomic welfare (Carter et al., 2014; Meek, 2011), human establishment of educational or wildlife conservation or management institutions (Dressel et al., 2018; Hessing-Lewis et al., 2018), and human interactions and changes to policy discernible at the community or the societal level (Duvall et al., 2017). In comparison, the less observable or microscale outcomes of HWIs, such as the activities, behavior, and health of individual wildlife, and the psychological states, attitudes, experiences, and health of individual people, have received less attention (Table 1:III). Notable exceptions are the linear but 'emergent' framework proposed by Morzillo et al. (2014), and particularly the nested, multilevel frameworks of Carter et al. (2017) and Lischka et al. (2018) (Table 2), which place stronger (than the other frameworks in Table 2) foci on the ecology and behavior of individual wild animals (Carter et al., 2017; Lischka et al., 2018), the attitudes, perceptions and experiences of individual humans (all three studies), physiological indicators of individual wildlife (Lischka et al., 2018), and indicators of human mental health (Morzillo et al., 2014). Such individual effects are conceptualized as being impacted by HWIs, and as 'embedded' or 'nested' within other outcomes at higher organizational levels, specifically wildlife populations and ecosystems, and human communities and societies (illustrative examples have been reviewed in the previous section).

Understanding how the charactersistics and behavior of individual people impact, and are impacted by, HWIs remains a particularly major gap in the literature (Table 1:III). Only recently has there been a focus on how aspects, characteristics and role of individual people impact HWIs studies, and which argue that an effective understanding of HWIs require assessments of the diverse viewpoints and behaviors of stakeholders, conservationists, and policy makers (Woodroffe et al., 2005; Kansky et al., 2014, 2016). The consequential emergence of the subfield of 'conservation psychology' emphasizes that HWIs and their impact on humans may be influenced by a combination of individuals' psychological states (e.g., beliefs, emotional experiences, individual differences in perception and temperament, propensity to anthropomorphize), socioeconomic status (e.g., livelihood, access to education), demographic attributes (e.g., age, gender, sizes of family units), and contextual features of the anthropogenic environment (e.g., establishment of educational and/or policy-making institutions) (Kansky et al., 2014, 2016; Waytz et al., 2014). These approaches tend to conceptualize individual human behavior in terms of people's attitudes and degrees of tolerance towards wildlife, with specific behavior as emergent from the costs-to-benefits tradeoffs that they directly experience or perceive (Kansky et al., 2014, 2016). Through collecting self-reported data on human demographics, behavior, and experiences with wildlife, empirical tests of these 'wildlife tolerance models', and similar conservation psychological frameworks, have quantified individual human behavior in the context of HWIs involving wildlife taxa such as large carnivores, black bear, elephants, ungulates, and nonhuman primates (reviewed in Kansky et al., 2014, 2016). Meta-analyses of these data revealed that human tolerance and positive attitudes about wildlife were strongly influenced by inter-individual differences in perceptions of (particularly) intangible costs and benefits, with the latter also being influenced by peoples' taxonomic bias (e.g., preference for elephants and nonhuman primates) and demographic characteristics (farmers, compared to urban residents, were more tolerant independent of their perceived extent of damages) (Kansky et al., 2014, 2016).

Decades of psychological research demonstrate that human self-reports often do not map on to people's behavior, that people maybe unaware of components of their own mental life, and that aspects of mental life such as beliefs and attitudes may have articulable (explicit) and inarticulable (implicit) components (Greenwald et al., 1998; Fazio and Olson, 2003; Frith and Frith, 2008; Nisbett and Wilson, 1977; Dang et al., 2020). Thus, conservation psychological approaches that combine self-reported data with behavioral observations and experimental data of peoples' response time and accuracy to comprehensively evaluate both explicit and implicit sources of bias of individual people need to be integrated into human-wildlife CNHS frameworks.

Indicators of human and wildlife health are also hidden outcomes that remain under-addressed in human-wildlife CNHS studies (Table 1: III). Integrating health outcomes into CNHS frameworks is vital since these effects may underlie or predict more observable outcomes such as human and wildlife reproductive success, fitness, and survival. In wildlife, interactions with humans or anthropogenic factors have been associated with physiological changes that indicate heightened stress levels (Marechal et al., 2011; Tennessen et al., 2014), but also increased energy levels on account of consuming human foods of high calorific value (Lischka et al., 2018). Conversely, interactions with wildlife can negatively impact human mental health through the imposition of transactional and opportunity costs that may result in increased alcohol consumption, loss of sleep, and post traumatic stress disorder (PTSD) (Barua et al., 2013), but can also positively impact mental health through generating an increase in livelihood and economic benefits through activities like tourism that generate upliftment (Carter et al., 2014).

Another major health outcome of HWIs is cross-species transmission of zoonotic disease. Human activities and behavior that increase direct contact with wildlife, or increased wildlife exposure to human-modified landscapes and contaminated food or water sources, may affect in the transmission of pathogens into wildlife systems, leading to rapid outbreaks and related population declines (Nunn et al., 2008). Conversely, many wildlife species are also reservoirs of zoonotic agents that pose a serious threat to humans, livestock, and other wildlife (Cunningham et al., 2017). The impact of disease transmission from wildlife is particularly relevant now, as SARS-CoV-2, the virus that causes COVID-19 originated in bats and likely jumped to human wet-markets in Asia – a particular kind of HWI (Gryseels et al., 2020). Following the COVID-19 pandemic, HWIs will continue to be at the forefront of research on zoonotic transmission, and specifically emerging infectious agents which are among the most critical global health issues today (Cunningham et al., 2017; Nunn et al., 2008; Gryseels et al., 2020).

The lack of cross-site comparative studies of HWIs (Table 1:IV) has also only been partly addressed by the existing human-wildlife CNHS frameworks. Indeed, most studies reviewed in Table 2 have proposed a single, unique type of CNHS framework that is specific to either the wildlife taxonomic group (e.g., polar bears: Meek, 2011; greater sage-grouse: Duvall et al., 2017) or their social-ecological role (e.g., carnivores affecting ecosystem services: Carter et al., 2017). A few more generic human-wildlife CNHS frameworks have been constructed (Carter et al., 2014; Morzillo et al., 2014; Lischka et al., 2018), but these have been illustrated for either a single wildlife taxon or human-wildlife system (e.g., rodents as urban pests: Morzillo et al., 2014; black bears as peri-urban generalist omnivores: Lischka et al., 2018), or for up to two human-wildlife systems in which the wildlife taxa have similar social-ecological roles (e.g., tigers and giant pandas as keystone species: Carter et al., 2014; tigers and wolverines as carnivores: Carter et al., 2017). Although a few studies discuss the need for comparative studies of HWIs as CNHS (Carter et al., 2014, 2017; Morzillo et al., 2014; most notably Lischka et al., 2018), there is currently a lack of adherence to a standardized nomenclature of CNHS components *across* these studies, which may stem from inconsistencies regarding the structuring and categorization of what variables constitute a typical CNHS/SES system more generally (Colding and Barthel, 2019). Addressing this lack of adherence to a standard nomenclature would constitute a critical first-step towards conducting comparative human-wildlife CNHS research (Table 1:IV).

7. An integrated conceptual framework for human-wildlife CNHS

Here we present a generic, conceptual framework for human-wildlife CNHS (Fig. 3). This 'integrated framework' uses elements from the previous, largely taxon- or system-specific (in their focus and/or illustration) human-wildlife CNHS frameworks that we review earlier (Table 2). We also build on these previous efforts in two important ways. First, we place a greater emphasis on the nested or embedded nature of microscale, subtle CNHS outcomes in individual humans and wildlife that remain under-represented or under-evaluated in HWI and CNHS research (Table 1:III). We do so by classifying CNHS outcomes based on both their organizational level (as in previous frameworks by Carter et al., 2017 and Lischka et al., 2018) and their discernibility (described below) (Fig. 3), through the integration of (i) conservation psychological approaches that consider people's psychology holistically (including self-reported explicit features, implicit features, and behavior), and (ii) human and wildlife health outcomes. Second, we attempt to standardize the designation and nomenclature of the major components of human-wildlife CNHS through this framework, by more clearly (compared to previous frameworks) defining and distinguishing between the major CNHS components. As we state earlier, this is critical in order to establish CNHS as providing a platform or basis for comparative studies of HWIs (Table 1:IV), that also eventually move human-wildlife CNHS research and frameworks from conceptual to operational (see the following 'Discussion' section).

We suggest that all aspects of human-wildlife CNHS may be classified into one of six major CNHS components: (1) *attributes* and *features*, which are 'predictor' variables related to both individual wildlife and people, as well as group, societal, and environmental-context-level predictors (that is, predictors have a multi-level structure and may be nested within each other), (2) *human-wildlife interactions and experiences*, (3) *feedback mechanisms and processes*, (4: 2 & 3 together) *between-systems couplings*, (5) *outcomes*, and (6) *within-systems couplings* (Fig. 3). Our intent behind constructing this framework is to integrate the components of previous CNHS frameworks of HWIs, to establish CNHS as a broadly applicable, theoretical framework with a standardized designation/nomenclature of components to conduct fundamental research on HWIs.

Attributes and *features* refer to the intrinsic characteristics of wildlife or humans involved in conflict (Lischka et al., 2018), and extrinsic components pertaining to the natural and anthropogenic environment respectively (Morzillo et al., 2014; Hessing-Lewis et al., 2018). Attributes may include the demographic characteristics (e.g., age, sex), genotype, and personality-type of individual humans and wildlife, wildlife population- or species-wide evolutionary history, and/or prior history of exposure/experience to HWIs, and human population or community demographics such as cultural history and socioeconomic background (Lischka et al., 2018). These features relate to different levels of analysis (individual, group) and are included in the framework at the appropriate level such that individual level attributes may be nested within group level attributes. In addition, explicit (articulatable) and implicit (not articulatable) features of humans related to their tendencies to anthropomorphize, perceive other beings as agents, and empathize, as well as

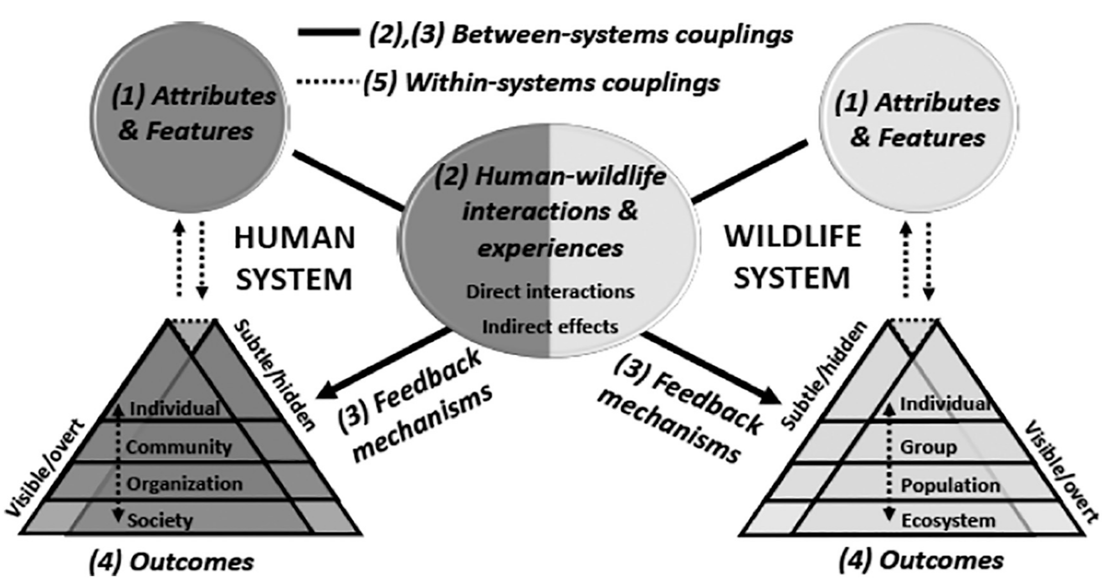

Fig. 3. An integrated conceptual framework of human-wildlife CNHS.

people's prior knowledge/regard for wildlife, would also constitute human attributes (Greenwald et al., 1998; Gray et al., 2007, 2012; Kansky et al., 2016). Natural features of the wildlife system include the distribution and abundance of resources, competitors, and/or predators (Dressel et al., 2018; Morzillo et al., 2014). Anthropogenic features include the distribution and abundance of human food and environmental contaminants, residential and commercial dwellings or buildings, educational, conflict-managing and/or policy-making institutions within the human system (Carter et al., 2014; Lischka et al., 2018; Morzillo et al., 2014). As with human and wildlife attributes, these features are ascribed to various levels of analysis and thus lend themselves to nested analyses.

One or more human and wildlife attributes and features may influence the dynamic nature and types of *HWIs at the interface* (see Introduction for a definition) (Meek, 2011; Carter et al., 2014; Lischka et al., 2018). We divide HWIs into two broad categories. *Direct behaviors* constitute interactions in which humans and wildlife may actively engage each other to affect changes in each other's space-use and/or behavior. In some cases, these may involve direct contact and/or transfer of biological materials (e.g., blood, saliva). These include human-to-wildlife aggression, provisioning, hunting, or trapping-and-relocation, and wildlife-to-human vigilance, aggression, predation, and stealing (summarized in Lischka et al., 2018; Nyhus, 2016). *Indirect effects* constitute those behaviors and actions of juxtaposed humans and wildlife that are directed towards one or more environmental features, that in turn affects changes in each other's' space-use and/or behavior. These include human depletion of wildlife ecosystem components (e.g., prey, competing species), destruction or fragmentation of wildlife habitat, and impact on abiotic environmental components (e.g., climate change, soil/water/noise pollution). Wildlife behavior such as foraging on urban waste or crops, predation on human livestock or pets, and spatial overlap or movement through human features like agricultural fields, also constitute indirect effects (summarized in Carter et al., 2014; Nyhus, 2016). Human sightings and experiences of wildlife through activities like tourism and conservation efforts would also fall into this category.

All HWIs may generate *reciprocal or feedback effects* on both human systems and wildlife systems, meaning that effects in the integrated framework are specified as being bidirectional. We define these as the context- or system-specific 'costs-benefits tradeoffs' experienced by humans on account of interactions with wildlife and wildlife on account of human activity. These tradeoffs may be resource-related or health-related, overt (more easily observed) or subtle (less easily observed). For instance, HWIs like habitat fragmentation and/or human provisioning of wildlife may generate observable costs to wildlife in the form of greater depletion of natural resources (Carter et al., 2014; Duvall et al., 2017), but also more subtle costs related to environmental stress (Hessing-Lewis et al., 2018) and infectious disease acquisition (Cunningham et al., 2017; Gryseels et al., 2020). In other systems and contexts, human provisioning of wildlife may be beneficial for wildlife, for instance, the high calorific value of human foods for more dietarily flexible species that thrive in (peri)urban environments (Lischka et al., 2018). In the human system, interactions with wildlife like aggressive behavior, destruction of property, and vigilance, may generate costs, both more observable injuries or damages (Dressel et al., 2018), but also more hidden or subtle transactional and opportunity costs that lead to poor mental health (Barua et al., 2013), and increased susceptibility to infectious disease (Cunningham et al., 2017; Gryseels et al., 2020). Interactions with wildlife may also be beneficial to humans insofar as they are experiences as positive or pleasant (Carter et al., 2014), increase access to natural resources or ecosystem services (Meek, 2011), and revenue through ecotourism (Carter et al., 2014).

Attributes and features of one system (wildlife or human) can affect the other system through HWIs. We thus define the *between-systems couplings* of the integrated framework as constituting both the HWIs and the feedback mechanism(s) (arrows in Fig. 3) they generate. Between-systems couplings may affect multiple *outcomes* in wildlife systems and human systems. Here we build on previous nested frameworks constructed by Carter et al. (2017) and Lischka et al. (2018), by classifying outcomes across two, non-mutually exclusive scales – based on both organizational level (individuals - > ecosystems (wildlife) or societies (humans); as in these nested frameworks) and their discernibility (hidden/subtle - > overt/obvious) (Fig. 3). For individual humans and wildlife, some hidden outcomes may be indicators of animal physiology and health, including changes to wildlife time and energy budgets and calorific intake (Lischka et al., 2018), wildlife stress-levels (Marechal et al., 2011), indicators of human mental health and stress such as loss of sleep and signs of PTSD (Barua et al., 2013), and the prevalence and diversity of infectious agents in both humans and wildlife (Cunningham et al., 2017; Nunn et al., 2008). Changes to foraging strategies, movement patterns, and spatial/social behavior of individual wildlife (Lischka et al., 2018), and the explicit attitudes, beliefs, and experiences of individual humans (Morzillo et al., 2014; Lischka et al., 2018; Kansky et al., 2016) are examples of behavioral outcomes that, although more overt than health outcomes, are nonetheless subtle and challenging to detect. Among the most observable outcomes may be indicators of wildlife fitness and survival as gauged by animals' reproductive output, lifespan, and offspring survival (Carter et al., 2017; Lischka et al., 2018), and human lifestyle changes as indicated by household sizes (Carter et al., 2014), income (Carter et al., 2014), or private ownership of goods and services (Dressel et al., 2018; Hessing-Lewis et al., 2018).

As demonstrated in the nested human-wildlife CNHS frameworks (Carter et al., 2017; Lischka et al., 2018), individual-level outcomes may simultaneously underlie and be influenced by outcomes at higher organizational levels. For instance, changes to individual behavior, health, and fitness may be linked to the composition, sizes, and social or genetic structure of wildlife groups and populations (Lischka et al., 2018), and in-turn other biotic components of wildlife ecosystems (Carter et al., 2014; Dressel et al., 2018; Hessing-Lewis et al., 2018; Lischka et al., 2018). Likewise, changes to the physical and mental health, attitudes beliefs and experiences, and lifestyles of individual people may affect the regulation and sharing of resources and cooperative interactions at the community level (Dressel et al., 2018; Hessing-Lewis et al., 2018), effective policy-making by educational, conservational or resource management units that advance the overall socio-economic growth of societies (Carter et al., 2014; Meek, 2011).

Finally, human and wildlife outcomes at various organizational levels of analysis, may also be directly impacted by constituent components (attributes and features) within the same (human or wildlife) system. For instance, animals' demographic characteristics (e.g., age, sex) may interact with natural features of their environment (e.g., abundance of resources, predators) to directly influence the behavior, health, and fitness of wildlife (Carter et al. 2015, 2017; Lischka et al., 2018). Within the human system, conservation psychological approaches conceptualize how implicit factors (e.g., tendency to anthropomorphize or ascribe minds to other agents) may combine with explicit features of both individual people (sociodemographic factors like age, gender, employment status) and the anthropogenic environment (e.g., prevalence of educational and policy-making institutions) to directly influence human attitudes, behavior, and social conflict (Kansky et al., 2014, 2016). The integrated framework accounts for the interdependency of outcomes and the effects of implicit and explicit attributes and features on outcomes, within the same (wildlife or human) system, as *within-systems couplings*.

8. Discussion and future directions

In summary, the integrated CNHS framework provides a platform to address all four challenges facing research on HWIs (Table 1). Like these previous CNHS frameworks reviewed earlier, this framework places a balanced emphasis on human and wildlife components (Table 1:I). Through its explicit definition and designation of attributes, features, between-, and within-systems couplings, the framework also accounts for the multiple (rather than single) types of components and mechanisms that may underlie HWIs and their outcomes (Table 1:II). In addition, the integrated framework expands on previous versions in important ways. First, we build on previous hierarchical frameworks that placed a greater emphasis on hierarchical/organizational levels of outcomes (Morzillo et al., 2014; Carter et al., 2017; Lischka et al., 2018), by additionally defining and classifying CNHS outcomes based on their discernibility (overt/visible - > hidden/subtle) (Fig. 3). We emphasize that inclusion and distinction of human implicit states and explicit outcomes, and a greater focus on human and wildlife health outcomes, may both be critical additions to understanding HWIs as CNHS (Table I: III). Finally, through the consideration of a standardized nomenclature of CNHS components, the integrated framework provides a much-needed platform or basis for comparative studies (Table 1:IV).

The integrated framework offers the scope to assess aspects of human systems that are understudied in human-wildlife CNHS contexts. Specifically, it underscores the importance of evaluating whether people's experiences with wildlife, whether costly or beneficial, may interact with features of their own psychology and contextual features to influence outcomes related to their attitudes and beliefs, and interactions with policy-makers. With the introduction of conservation psychology, increasing interest has been paid to the behavioral aspects of HWIs, and specifically the human social and psychological factors that influence, and are in turn influenced by, our perceptions, tolerance, and attitudinal shifts towards wildlife (Kansky et al., 2014, 2016; Waytz et al., 2014; Amiot et al., 2017). People vary in the extent to which they ascribe human-like characteristics to other agents (i.e., their tendency to anthropomorphize), and believe that other agents have minds, can act independently, and are capable of experience (Gray et al., 2007; Waytz et al., 2014). Individual-level variability in anthropomorphism and mind perception can culminate in behaviors relevant to human-wildlife CNHS (Kansky et al., 2014, 2016). For example, agents (individual wild animals and other people) who are perceived to have minds are also perceived to be responsible for their actions (Gray et al., 2007) and humans are more likely to 'punish' such agents when they deviate from social norms (Gray et al., 2012). People who report higher propensity to engage in anthropomorphism, compared to those who score lower, report less endorsement of norms of harming other agents, greater concern for the environment, and greater ascription of social norms (Waytz et al., 2014). Features of mind perception (perceiving the extent to which an agent is capable of experience and perception) are related to the moral judgements that people make (Gray et al., 2012). So, an individual high in anthropomorphism may believe that animals are entirely responsible for their behavior and may therefore be less willing to change behavior towards wildlife.

The framework integrates the above domains of conservation and social psychology into human-wildlife CNHS, while making a clearer distinction (than previous frameworks that also placed stronger foci on the attitudes and behaviors of individual people: Lischka et al., 2018; Morzillo et al., 2014) between implicit components (CNHS attributes) and explicit factors (CNHS attributes and outcomes). We anticipate that implementing the integrated framework based on the above-described example, for instance, would entail assigning individual anthropomorphism and mind-perception as implicit *attributes* of the human system. These may influence experiences of humans with wildlife—that is HWIs – and may interact with such experiences (*between-systems couplings*) to generate, to varying extents, explicit changes to individuals' attitudes and behaviors (*outcomes*) that affect higher-order social outcomes like conflict management and policy change.

Our integrated CNHS framework also places a greater focus on assessing human and wildlife health outcomes. Epidemiological models are increasingly beginning to consider pathogen- and host-specific attributes, environmental factors, and heterogeneity in human and animal space-use overlap or contact rates, in modeling the acquisition and transmission of infectious agents (VanderWaal and Ezenewa, 2016; Nunn et al., 2008). The integrated framework, through its evaluation of HWIs and their effects on human and wildlife spatial and social behavior that may underlie disease transmission, naturally lends itself to the integration of epidemiological assessments. Within the wildlife system, the complex relationship between animal physiology, stress, and disease risk, may in turn impact observable outcomes such as individual reproductive output and survival. Similarly, within-systems effects within the human system could unravel the interactions (or lack thereof) between humans directly impacted by conflict, and higher-order organizations like hospitals and clinics that provide them with medical aid or compensation.

More generally, we anticipate that this integrated CNHS framework would provide a mechanistic platform or basis for One-Health (OH) studies that tend to simultaneously evaluate indicators of human, wildlife, and environmental health parameters (Cunningham et al., 2017; Murtaugh et al., 2017; Wilcox et al., 2019; Zinsstag et al., 2011). The rise of human-wildlife CNHS frameworks has also coincided with that of the OH approach (Cunningham et al., 2017; Murtaugh et al., 2017; Zinsstag et al., 2011). Conceptually similar to CNHS, OH promotes the idea that challenges surrounding human health issues cannot be dissociated from, and may in fact be strongly interlinked to, environmental health or from veterinary medical practices associated with treating wild and domestic animals. In other words, the health of humans, livestock, wildlife, and ecosystems need to be evaluated as an integrated whole in order to implement sustainable strategies that benefit both the environment and public alike (Cunningham et al., 2017; Zinsstag et al., 2011). Yet, OH is also different to CNHS in that it thus far lacks one or more clearly defined structural frameworks with regards to a consistent or standard designation of natural and human components (e.g., attributes, features, outcomes) and their interacting mechanisms and feedback effects (e.g., within-, between-systems couplings) that may underlie the emergence of health outcomes through between- and within-systems couplings. Recently, researchers have described how OH approaches, particularly in the context of understanding emerging infectious disease at the human-livestock interface, might benefit from implementing resilience-based SES/CNHS frameworks (Wilcox et al., 2019). Similarly, we anticipate that our inclusion of health outcomes into the integrated CNHS framework would provide OH studies focusing on human-wildlife interfaces a standardized, structural framework to assess health indicators as emergent outcomes of HWIs.

The integrated framework lends itself to comparative studies by using a standardized nomenclature of CNHS components (Table 1:IV). To demonstrate the potential of the integrated framework for comparative research (Table 1:IV), we attempt to categorize and fit the CNHS components described or evaluated in the illustrations of each of the eight previous human-wildlife CNHS frameworks reviewed earlier, into the categories of CNHS components presented in this framework (Table 3). Implementing CNHS frameworks to conduct cross-site comparisons of HWIs and their effects may be complicated by the multiple human and natural system components to evaluate, and by the dynamic nature of some CNHS components (Liu et al. 2008; Carter et al., 2014). We propose that a necessary 'first-step' towards gaining perspective of this complexity would be to recognize, and subsequently categorize, the operational measures and mechanisms of HWIs and their effects into a standardized set of comparable components. Our categorization and fit of the operational measures and mechanisms of previous human-wildlife CNHS studies into the terminology of this integrated framework serves the dual purpose of illustrating the broad scope of the integrated framework, and its provision of a platform for future studies attempting to conduct cross-CNHS comparisons (Table 1:IV). With regards to the latter, it may inform choice(s) of future human-wildlife CNHS studies, by carefully considering whether and which wildlife system or human system components are similar, versus different, across systems (Ceauşu et al., 2019). Indeed, such baseline comparisons of human-wildlife CNHS across wildlife taxa of similar ecological roles (e.g., apex predators: Carter et al., 2017), versus different ecological roles and/or

Table 3
The fit of the major components and interlinkages of previous human-wildlife CNHS frameworks into the integrated CNHS framework.

Study	Wildlife species	Between-systems couplings				
		(1) Attributes & Features (predictors)	(2) Human-Wildlife Interactions	(3) Feedback Mechanisms	(4) Outcomes	(5) Within-system Couplings
Carter et al. (2017)*	Tigers (*Panthera tigris*)	Wildlife/Natural System: Individual age & sex; habituation; population size; prey abundance Human System: Individual attitudes & experiences; availability of hunting resources; hunting policy-making	Indirect: (Reduced) human hunting of tiger prey Direct: Hunting/poaching	Wildlife/Natural System: Changes to prey & predator abundance Human System: Changes to the value/demand for animal parts	Wildlife/Natural System: Population declines Human System: Greater law enforcement; changes to poaching techniques	Wildlife/Natural System: Prey abundance linked to tiger predatory behavior Human System: Market demand linked to law enforcement, policy & poacher techniques
Carter et al. (2017)*	Wolverines (*Gulo gulo*)	Wildlife/Natural System: Individual age & sex; habituation; population size; den site predictability Human System: Individual attitudes and experiences; access to compensation; livelihood	Indirect: (Increased) wolverine hunting of reindeer (livestock) Direct: (Reduction in) Hunting/poaching	Wildlife/Natural System: Increase in animals & dens Human System: Compensation for dens & livestock loss	Wildlife/Natural System: Population increases; predictability in denning behavior Human System: Livelihood is maintained; changes to attitudes & behavior	Wildlife/Natural System: Population density linked to denning behavior and predation rates Human System: Compensation & performance payments linked to livelihood & well-being
Meek (2011)	Polar bears (*Ursus maritimus*)	Wildlife/Natural System: Species' history; habitat quality; sex Human System: Ethnography; interaction history; market demand	Indirect: Toxin accumulation; habitat loss Direct: Hunting	Wildlife/Natural System: Changes to home-range size Human System: Changes to policy	Wildlife/Natural System: Hunting & denning behaviors Human System: Indigenous subsistence; economic benefits; maritime activities; changes to policy	Wildlife/Natural System: Sex ratio linked to hunting & denning behavior, & reproductive success Human System: Demographics linked to maritime activities & economic policy
Duvall et al. (2017)	Greater Sage Grouse *(Centrocercus urophasianus)*	Wildlife/Natural System: Population distribution; abundance of flora; reproductive & rearing behavior Human System: Employment institutions	Indirect: Habitat fragmentation; competition Direct: Hunting	Wildlife/Natural System: Fluctuation in resource abundance Human System: Costs-benefits fluctuations	Wildlife/Natural System: Demographics Human System: Government-stakeholder interactions; inter-stakeholder interactions	Wildlife/Natural System: Foliage cover linked to grouse behavior Human System: Individual employment & knowledge linked to stakeholder activities
Hessing-Lewis et al. (2018)	Sea otters *(Enhydra lutris)*	Wildlife/Natural System: Distribution & abundance; seagrass communities; species richness Human System: Employment; perceptions & health; socio-cultural norms	Indirect: Habitat alteration; disease outbreak; harvesting sea-grass	Wildlife/Natural System: Seagrass resistance & abundance Human System: Benefits of fisheries & carbon storage	Wildlife/Natural System: Distribution, abundance & foraging Human System: Demographics, employment & quality of life	Wildlife/Natural System: Seagrass community (resource) distribution linked to otter abundance Human System: Cultural background & market availability linked to employment & quality of life
Dressel et al. (2018)	Moose (*Alces alces*)	Wildlife/Natural System: Population density, predators & competitors Human System: Socioeconomic characteristics; leadership; interaction history	Indirect: Browsing Direct: Collisions & shooting	Wildlife/Natural System: Ratio of moose to other species Human System: Damages; frequency of meat consumption	Wildlife/Natural System: Demographics; foraging Human System: Moose-Management Units; forestry ownership	Wildlife/Natural System: Resource abundance, predators & competitors linked to population density Human System: Forestry availability and ownership linked to socioeconomic & leadership activities
Carter et al. (2014)*	Tigers (*Panthera tigris*)	Wildlife/Natural System: Vegetation density & species-diversity; prey abundance Human System: Socioeconomic background; locals vs tourists; farmer density; family sizes	Indirect: Habitat fragmentation Direct: Predation	Wildlife/Natural System: Reduction in prey abundance Human System: Regulated resource collection	Wildlife/Natural System: Population fluctuations Human System: Family-planning; collaborations between institutions	Wildlife/Natural System: Prey abundance linked to tiger predatory behavior Human System: Employment opportunities linked to resident incomes
Carter et al. (2014)*	Giant pandas (*Ailuropoda melanoleuca*)	Wildlife/Natural System: Bamboo tree density; elevation; earthquakes Human System: Ethnic background; livelihood; family sizes; schools & services; forest management	Indirect: Habitat fragmentation	Wildlife/Natural System: Changes to resource distribution Human System: Costs incurred	Wildlife/Natural System: Foraging behavior; Demographics & viability Human System: Land-use changes; zoning schemes; policy changes	Wildlife/Natural System: Natural resource abundance linked to foraging behavior Human System: Policy-making institutions linked to resident incomes
Morzillo et al. (2014)	Rodents Order: *Rodentia*	Wildlife/Natural System: Landscape features; rodent species-type & abundance; prevalence of predators Human System: Landscape features;	Direct: Outdoor observation of rodents; pest control behavior	Wildlife/Natural System: Exposure to "rodenticides" Human System: Exposure to "rodenticides".	Wildlife/Natural System: Demographics; predator prevalence Human System: Individual attitudinal shifts; Individual or household	Wildlife/Natural System: Predator presence linked to rodent demographics and density Human System: Urban landscape features

(*continued on next page*)

Table 3 (*continued*)

Study	Wildlife species	Between-systems couplings				
		(1) Attributes & Features (predictors)	(2) Human-Wildlife Interactions	(3) Feedback Mechanisms	(4) Outcomes	(5) Within-system Couplings
		interaction history; socioeconomic characteristics			welfare; alterations to urban landscape features	linked to individual attitudes & motivations
Lischka et al. (2018)	Black bears (*Ursus americanus*)	Wildlife/Natural System: Resource distribution; sociodemography; physiology; boldness Human System: Sociodemography; experience; values & emotions; garbage distribution	Indirect: Foraging on garbage Direct: Bear sightings	Wildlife/Natural System: Foraging time & caloric intake Human System: Vigilance of bear attacks	Wildlife/Natural System: Hibernation time; reproductive output Human System: Attitudes to bear management actions; thrash management; home-ownership associations	Wildlife/Natural System: Resource abundance linked to bear abundance, reproductive behavior & hibernation Human System: City infrastructure and policy-making institutions linked to individual attitudes, values, & garbage-management

[*] studies repeated twice, one for each of two human-wildlife systems on which they illustrated their CNHS framework.

conservation statuses (e.g., terrestrial forest carnivores versus (peri) urban omnivores: Table 3), may inform the design and implementation of interventions that may be more universally applicable across species and contexts, versus those that need to be specifically catered to certain human-wildlife interfaces.

We note that one critical gap in the human-wildlife CNHS literature pertains to the lack of quantitative or analytical models. A few generic conceptual frameworks that we review here have been illustrated using findings from pre-existing, non-CNHS quantitative studies that each analyzed the relationship(s) between a sub-set of human and wildlife components represented in the CNHS framework (Carter et al., 2014, 2017; Morzillo et al., 2014; Lischka et al., 2018). Other taxon-specific frameworks were constructed by including an exhaustive set of variables which were operationalized in the same study (e.g. from human interviews: Duvall et al., 2017), in pre-existing studies on the same human or wildlife system (e.g. polar bear ranging and foraging behavior: Meek, 2011), and/or included to facilitate future, quantitative evaluations of a human-wildlife system as CNHS (e.g. the impact of sea-otter foraging on human societal variables: Hessing-Lewis et al., 2018). Finally, recent attempts to move human-wildlife CNHS from conceptual to operational offer step-wise descriptions of implementing these frameworks (Ceausu et al. 2019). In summary, all these previously constructed frameworks and reviews, including this one, stop short of illustrating how human-wildlife CNHS can be quantified as integrated 'whole' systems. Quantitative methods like network analysis (Gonzales and Parrott, 2012), agent-based modeling (An, 2012), and (more recently) structural equation modeling (Allen et al., 2020) are now increasingly being recognized as being powerful tools to operationalize CNHS as 'whole' systems. A discussion of the quantitative tools that can be implemented to evaluate CNHS frameworks is beyond the scope of this review, but testing different tools and evaluating their efficacy in the context of CNHS approaches is an important direction for future research. In this light, there is now a pressing need for human-wildlife CNHS frameworks, through implementing such approaches, to move from being qualitative to quantitative in their demonstrative scope.

9. Conclusions

Reconciling human's and wildlife's needs in order to move from conflict to coexistence presents some of the most pressing, globally important challenges of modern times. Our review highlights how CNHS approaches is especially useful to address some of the major gaps and challenges that underlie fundamental research on HWIs. Building and consolidating previous attempts into a broad, integrated conceptual CNHS framework with standardized nomenclature, we establish, in this review, the utility of CNHS in addressing these challenges, as providing a broadly applicable platform or basis for evaluating HWIs and their outcomes. We discuss the scope of this integrated framework as providing a theoretical platform for conducting future quantitative assessments that addresses critical gaps in research on HWIs, specifically the hidden/subtle aspects HWIs related to human psychological states and human and wildlife health outcomes, and comparative assessments of HWIs as CNHS. We anticipate that the continued implementation of CNHS would enable more unbiased, data-driven, and quantitative outcome-based assessments of the extent to which HWIs lead to conflict or coexistence between human and wildlife, and indeed within human communities impacted by HWIs. In doing so, they may profoundly impact long-term projections of human and wildlife survival, as well as the design and implementation of conservation- or conflict-managing interventions and strategies as may be necessary.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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